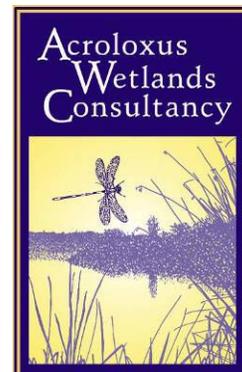


Texada Stickleback Species Pair Recovery Group

Critical Habitat Survey for Threespine Stickleback Species Pairs: Aquatic Vegetation Mapping in Priest and Paxton Lakes, Texada Island, BC

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EXECUTIVE SUMMARY

Threespine sticklebacks are distributed throughout coastal environments across northern hemisphere. Despite their adaptation to a wide variety of habitats, there are very few instances of two separate species co-occurring in shared waters. In fact, such sympatric species of sticklebacks are known to have evolved independently in only five separate water drainages in one region, the central Strait of Georgia in coastal British Columbia, Canada. What determines their limited distribution is still not well understood. Geological history has doubtless played a role in promoting the divergence and persistence of the species pairs, but specific ecological and physical attributes of lakes are also likely important determinants of their local distribution. These factors include the community structure of the lake. For example, aquatic vegetation communities likely play an important role not only in maintaining healthy stickleback population sizes but also in minimizing hybridization events between the sympatric species, ensuring the integrity of the species pairs.

As a first step to improving our understanding of the importance of the aquatic plant community structure to the evolution and conservation of the benthic-limnetic stickleback species pairs, we surveyed and mapped the aquatic vegetation of Priest and Paxton lakes on Texada Island, BC; the first survey of its kind in these waters. We found that the majority of the littoral fringes of both Priest and Paxton lakes are occupied by both reed and macrophyte beds. The composition of macrophyte beds varied somewhat between lakes; however, it is perhaps the similarities between them that are more striking and most significant to the persistence of the stickleback species pairs. For example, they share a preponderance of a species of *Chara* amongst the most common and dominant macrophyte.

This work can now serve as a baseline to monitor the health of existing macrophyte beds through regular surveys of the macrophyte beds within each lake. Such observation can act as an early warning system about the health of the lakes and will serve as an important conservation tool in maintaining the integrity of the species pairs. These surveys will also act as a baseline to conduct comparable surveys in other stickleback lakes, from which we can build our understanding of the role played by the abundance and composition of macrophytes in the evolution and persistence of benthic limnetic species pairs.

TABLE OF CONTENTS

SUMMARY	I
2.0 METHODOLOGY	3
2.1 Lake Surveys.....	3
3.0 RESULTS	4
3.1 Composition of Priest and Paxton lakes shorelines	4
3.2 Composition of macrophyte beds.....	4
4.0 DISCUSSION.....	11
5.0 REFERENCES	11
6.0 APPENDICES.....	14
Appendix A: Specimen of <i>Chara</i> sp.....	14
Appendix B: Specimen of <i>Najas flexilis</i>	15
Appendix C: Specimen of <i>Potamogeton amplifolius</i>	16
Appendix D: Specimen of <i>Potamogeton gramineus</i>	17
Appendix E: Specimen of <i>Potamogeton praelongus</i>	18
Appendix F: Specimen of <i>Potamogeton robbinsii</i>	19
Appendix G: Specimen of <i>Potamogeton zosteriformis</i>	20
Appendix H: Specimen of Thin grass	21
Appendix I: Specimen of <i>Utricularia vulgaris</i>	22
Appendix J: Map of macrophyte beds containing <i>Chara</i> in Priest and Paxton lakes, Texada Island, BC.....	23
Appendix K: Map of macrophyte beds containing <i>Najas flexilis</i> in Priest and Paxton lakes, Texada Island, BC.....	24
Appendix L: Map of macrophyte beds containing <i>Potamogeton amplifolius</i> in Priest and Paxton lakes, Texada Island, BC.	25
Appendix M: Map of macrophyte beds containing <i>Potamogeton gramineus</i> in Priest and Paxton lakes, Texada Island, BC.	26
Appendix N: Map of macrophyte beds containing <i>Potamogeton praelongus</i> in Priest and Paxton lakes, Texada Island, BC.	27
Appendix O: Map of macrophyte beds containing <i>Potamogeton robbinsii</i> in Priest and Paxton lakes, Texada Island, BC.	28
Appendix P: Map of macrophyte beds containing <i>Potamogeton zosteriformis</i> in Priest and Paxton lakes, Texada Island, BC.	29

Appendix Q: Map of macrophyte beds containing Thin grass in Priest and Paxton lakes, Texada Island, BC..... 30

Appendix R: Map of macrophyte beds containing *Utricularia vulgaris* in Priest and Paxton lakes, Texada Island, BC.... 31

LIST OF FIGURES

Figure 1: Map of reed and macrophyte beds in Priest Lake, Texada Island, BC.....	5
Figure 2: Map of reed and macrophyte beds in Paxton Lake, Texada Island, BC.....	6
Figure 3: The length of Priest and Paxton lakes shoreline, reed and macrophyte beds.....	7
Figure 4: The proportion of Priest and Paxton lakes shoreline occupied by reed and macrophyte beds.	7
Figure 5: Histogram illustrating the proportion of macrophyte beds occupied by each species.	10

LIST OF TABLES

Table 1: Priest Lake macrophyte bed composition.....	8
Table 2: Paxton Lake Macrophyte bed composition	9

1.0 INTRODUCTION

Threespine sticklebacks (*Gasterosteus spp.*), found across the northern hemisphere, have undergone an amazingly adaptive radiation since the last Ice Age. At this time, marine stickleback, which inhabit near shore coastal waters, became isolated in lakes as the land rose due to isostatic rebound following glacial retreat. Since that time, over 10 000 years ago, these stickleback have continued to evolve, adapting to their different lacustrine habitats through natural selection. This has most often resulted in sticklebacks within lakes remaining as one breeding unit whilst diverging from their marine ancestor. In a few instances, however, this process resulted in the evolution of two separate species within the same lake (Rundle *et al.* 2000).

These sympatric species of sticklebacks are known to have evolved independently (Taylor & McPhail 1999) in only five separate water drainages in the central Strait of Georgia region of coastal British Columbia in Canada: Enos Lake on Vancouver Island; the Vananda Creek drainage, including Priest Lake, on Texada Island; Paxton Lake on Texada Island; Hadley Lake on Lasqueti Island (McPhail 1993); and Little Quarry Lake on Nelson Island (Gow *et al.* 2008). In each pair, the limnetic stickleback is a small, slender fish that specializes in feeding on zooplankton in the open water zone of lakes. The benthic stickleback is larger and deeper-bodied, foraging mainly on large invertebrates from sediment or plants in littoral habitats (Schluter & McPhail 1992). Their divergence has occurred ultimately as a consequence of adaptation to alternative environments (Rundle *et al.* 2000). Their limited distribution, however, raises the question: if divergent natural selection for different ecological niches has driven their divergence, why have more species pairs not been found?

Details of the pairs' origins are still not well understood. An earlier description of the geological history of the Strait of Georgia suggested there had been two marine submergences separated by about 2000 years since the last glaciation (Mathews *et al.* 1970). This led to the idea that the same marine stickleback species (*Gasterosteus aculeatus*) had simply colonized each lake twice at intervals (the "double invasion hypothesis"; Schluter & McPhail 1992; McPhail 1993; Taylor & McPhail 2000). This scenario explained not only the highly restricted geographic distribution of the species pairs but also the narrow elevation range (50 to 100 m above sea level) of coastal lakes containing them (McPhail 1993; Vamosi 2003). However, more exhaustive geological samples have ruled out a second postglacial sea level rise in this region (Hutchinson *et al.* 2004) and, therefore, the scenario for the origin of the pairs based upon it. The species pairs nevertheless appear to have resulted from multiple invasions to freshwater by the marine species. For example, nuclear DNA indicate that the limnetic species in each lake is closer genetically to the present-day marine species than is the benthic species (Taylor & McPhail 2000), and it retains a higher tolerance of salt water (Kassen *et al.* 1995).

Atop this uncertainty about the precise historical context of their evolution, specific ecological and physical attributes of lakes are hypothesized to promote the divergence and persistence of the species pair, determining their local distribution. These factors include lake size and depth, habitat diversity (littoral and deeper open water zones) and depauperate fish communities (McPhail 1993; Vamosi 2003). Whilst the role of interspecific resource competition in the origin and maintenance of the divergence of the species pairs has been established through extensive research (Bentzen & McPhail 1984; Schluter 1993, 1994, 1995, 2003; Schluter & McPhail 1992), the importance of other potential factors such as parasitism and habitat diversity remain largely speculative.

In addition to habitat diversity contributed by the physical structure of the lake (for example, shallow littoral shores as well deep open water), the community structure of the lake is likely critical to the maintenance of the species pairs. While the role of fish assemblages has been explored (Rundle *et al.* 2003; Vamosi &

Schluter 2004), little is known about the impact of the invertebrate and aquatic vegetation communities on the species pairs, although their significance to stickleback population dynamics in general has been established. For example, macrophytes influence the risk of predation and the availability of food resources for fishes (Persson & Crowder 1997). In particular, the early stickleback life-history stages that are especially vulnerable to predation because of their poorly developed body armor prefer to inhabit vegetated areas rather than open water littoral microhabitats (Sillett & Foster 2000), especially when predators are present (Lehriniemi 2005). Indeed, by providing shelter, macrophyte beds likely fulfill an important nursery function for the stickleback species pairs.

Adult benthic sticklebacks' also show a preference for more complex substrate, including vegetated areas, due to the higher densities of refuge-seeking macro-invertebrates that they harbor (Webster & Hart 2004). In addition to functioning as larders, macrophyte cover is also beneficial to adult stickleback reproductive success (Kraak et al. 1999, 2000). Specifically for the species pairs, macrophytes also provide differentiated littoral microhabitats which the limnetic and benthic adults distinguish between in their preferred nesting areas (Ridgway & McPhail 1987). This microspatial segregation during the breeding season, when they share the littoral zone, contributes to the reproductive isolation of the species pairs (Ridgway & McPhail 1984).

Macrophytes, therefore, likely play an important role not only in maintaining healthy stickleback population sizes but also in minimizing hybridization events between benthics and limnetics, ensuring the integrity of the species pairs. This will depend not only on macrophyte abundance but also on their composition. For example, macrophytes differ in the chemical compounds they release into the environment, which may in turn affect their attraction to stickleback. For instance, the avoidance of *Ceratophyllum demersum* compared to *Chara tomentosa* by stickleback is likely due to repellent compounds produced by the former (Lehriniemi 2005). Preferences such as this have implications for the evolution of the species pairs; perhaps only lakes supporting suitable macrophyte communities have been able to support the divergence and maintenance of the species pair. This also has important implications for species pairs' conservation, with the preservation of current macrophyte beds likely important to sustaining the integrity of the species pairs.

Indeed, human-induced changes in the macrophyte environment can force sticklebacks to breed in non-preferred habitats (Candolin & Salesto 2006) and reduce the intensity of sexual selection (Candolin et al 2007). For the benthic-limnetic species pairs, this could lead to increased hybridization and jeopardize the integrity of the species pair. Indeed, there is now strong evidence that the disruption of the environmental factors underlying the origin of the species pairs can lead to the reversal of the benthic-limnetic divergence. In Enos Lake, elevated levels of gene flow associated with the appearance of an exotic crayfish (*Pascifasticus lenisculus*) during the 1990's have resulted in their collapse into a hybrid swarm (Gow et al. 2006; Taylor et al. 2006). Although the precise mechanism for this demise is unknown, the most obvious possible mechanism is the destruction of aquatic vegetation by crayfish, and associated increases in turbidity, compromising the potential for microhabitat segregation during the breeding season, leading to less accurate mate recognition and hybridization (Taylor et al. 2006).

The increased pressure on these species pairs and their habitat in these coastal areas, which are experiencing rapid increases in human population density, is further exemplified by the extinction of another of the known species pairs. The Hadley Lake species pair on Lasqueti Island was exterminated sometime between 1988 and 1992 following the unauthorized introduction of an exotic catfish, the brown bullhead (*Ameiurus nebulosus*, Hatfield 2001). With only three extant species pairs remaining on two islands, Texada and Nelson Islands, these unique fish are now considered endangered (COSEWIC 2000).

Our understanding of the factors important to the origin and maintenance of the species pairs is, therefore, of paramount importance. As a first step to improving our understanding of the importance of the aquatic plant community structure to the evolution and conservation of the benthic-limnetic stickleback species

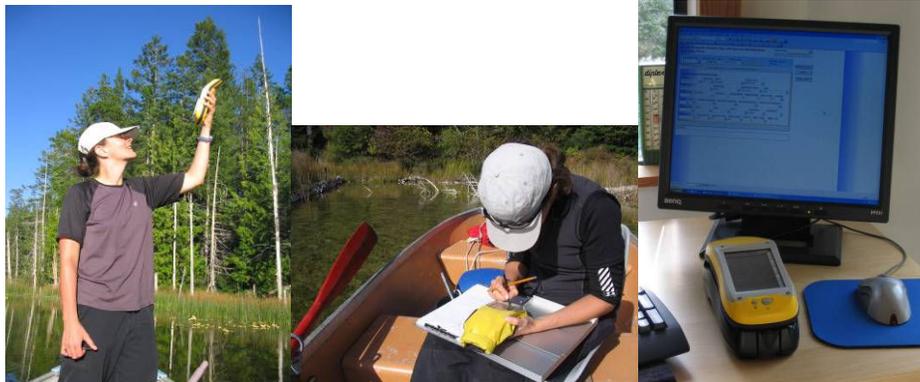
pairs, we surveyed and mapped the aquatic vegetation of Priest and Paxton lakes on Texada Island, BC; the first survey of its kind in these waters. This will serve as an essential baseline for future research and monitoring.

2.0 METHODOLOGY

2.1 Lake Surveys

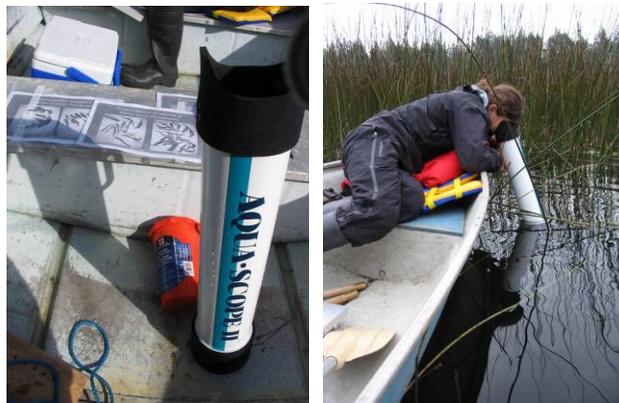
Three rounds of lake surveying were carried out during October 2006, August 2007 and October 2007. An initial reconnaissance of each lake involved collecting samples of macrophyte species present using a garden rake attached to a length of rope. These specimens were placed in plastic Ziploc bags for later identification and archiving. The specimens were preserved in a plant press and vouchers were mounted on herbarium sheets.

The outer perimeters of reed beds and macrophyte beds were then mapped by tracking them with a handheld Trimble GeoXT GPS Receiver. An AquaScope II bathyscope enabled underwater viewing of the macrophyte beds. GPS data was then transferred in digital form for analysis in ArcMap 9, Microsoft Pathfinder Office.



GPS data collection in the field is transferred to Culex database for mapping and analysis

Lastly, the bathyscope was used to conduct a detailed survey of species composition of every macrophyte bed in each lake, with the presence and dominance of species being noted.



Bathyscope aids species identification within macrophyte beds

3.0 RESULTS

3.1 Composition of Priest and Paxton lakes shorelines

With 4340m of shoreline (including a small island), Priest Lake has over a third more littoral fringe than Paxton Lake, which has 2790m. Approximately two thirds of each lake's shoreline is occupied by reed bed stands (3100m or 71% for Priest Lake, Fig. 1; 1820m or 65 % for Paxton Lake, Fig. 2; Figs. 3 & 4).

The macrophyte beds occupy (either abutting the shore or the adjacent reed beds) less than two thirds of the Priest Lake shoreline (2410m or 56%, Fig. 1), while they occupy a higher proportion of the Paxton Lake shoreline (2220m or 80%, Fig. 2; Figs. 3 & 4).

3.2 Composition of macrophyte beds

Nine species of macrophytes were found in Priest Lake (Table 1, Appendices A to I) and all but two of these were also documented in Paxton Lake (Table 2). While macrophyte beds were typically composed of four species in Paxton Lake, the number of species per macrophyte bed ranged from one to seven (Table 1). An average of five species was found per macrophyte bed in Paxton Lake, with species composition ranging from four to six (Table 2).

Tables 1 & 2 and Figures 4 to 12 highlight the distribution of each macrophyte species. Based on the proportion of total macrophyte beds occupied, Figure 13 illustrates which species are more widely distributed than others. In Priest Lake, *Urticularia vulgaris* and *Chara* were the most common species, closely followed by *Potamogeton amplifolius*. *Potamogeton robbinsii* and *Potamogeton gramineus* were intermediate in abundance whereas *Potamogeton praelongus*, *Potamogeton zosteriformis*, *Najas flexilis* and thin-leaved grass were less common.

In Paxton Lake, *Potamogeton amplifolius* and *Chara* were by far the most common species, closely followed by *Potamogeton zosteriformis* and *Urticularia vulgaris*. *Potamogeton gramineus* and *Najas flexilis* were intermediate in abundance while *Potamogeton praelongus* was rare.

Tables 1 & 2 and Figure 13 also highlight which macrophyte species tended to dominate each macrophyte bed. In Priest Lake, *Potamogeton robbinsii*, *Urticularia vulgaris* and *Chara* were the most dominant species. *Potamogeton praelongus*, *Potamogeton gramineus*, *Potamogeton amplifolius* and *Najas flexilis* were rarely dominant, while the remaining species, *Potamogeton zosteriformis* and thin-leaved grass, were never dominant.

As well as being the most common macrophyte species in Paxton Lake, *Potamogeton amplifolius* and *Chara* were clearly the most dominant species in Paxton Lake. *Potamogeton gramineus*, *Potamogeton zosteriformis* and *Urticularia vulgaris* were rarely dominant, while the remaining species, *Potamogeton praelongus* and *Najas flexilis*, were never dominant.

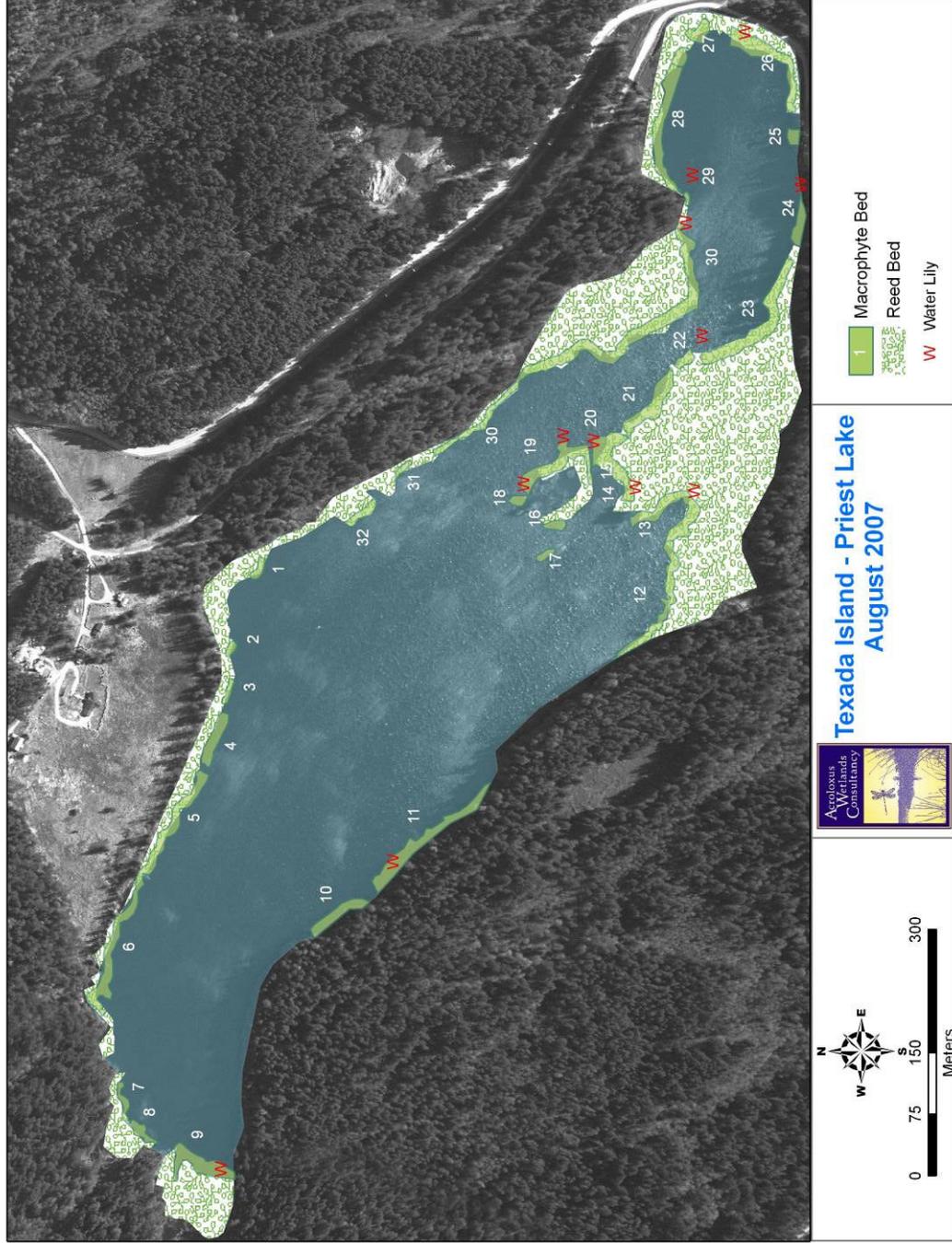


Figure 1: Map of reed and macrophyte beds in Priest Lake, Texada Island, BC.

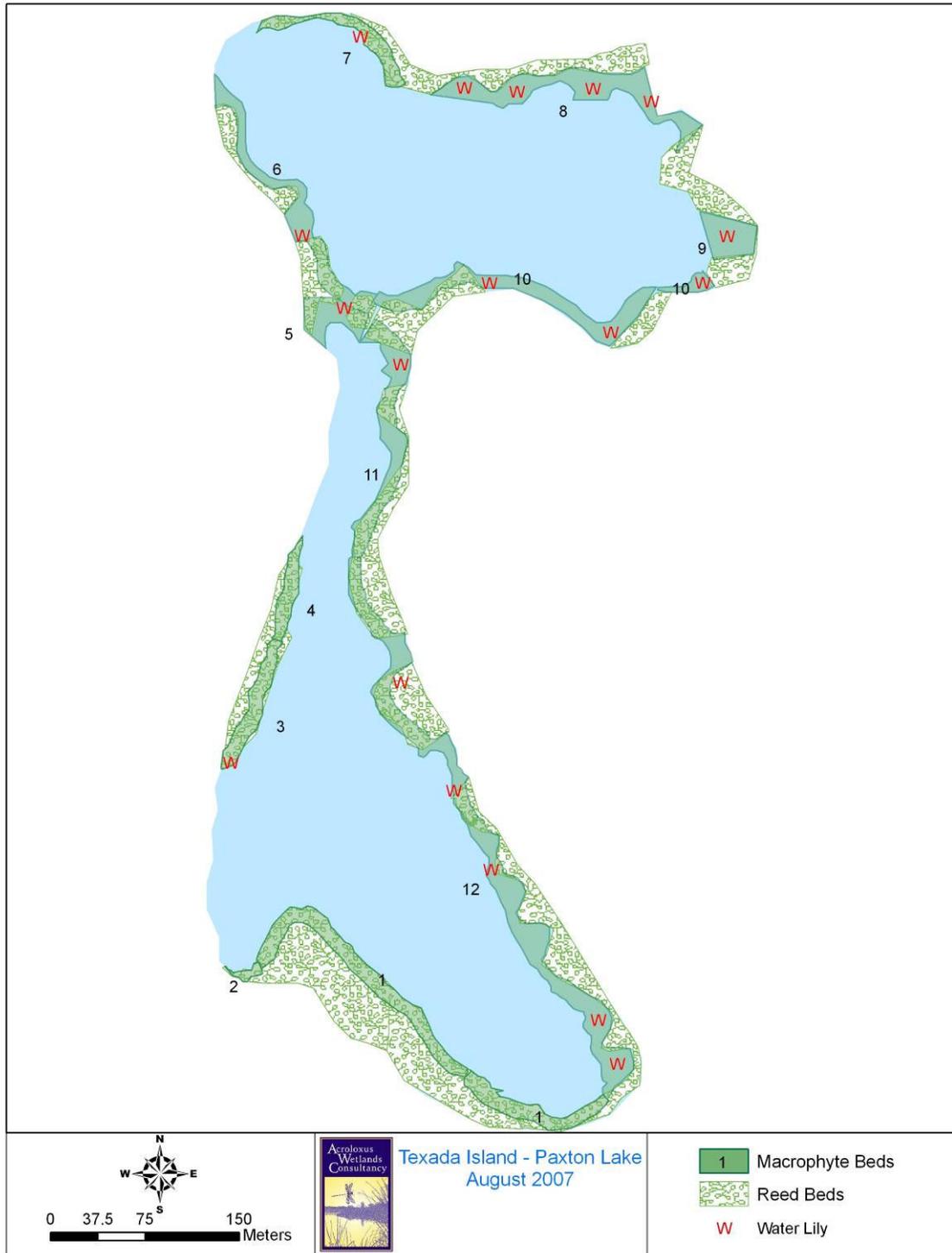


Figure 2: Map of reed and macrophyte beds in Paxton Lake, Texada Island, BC.

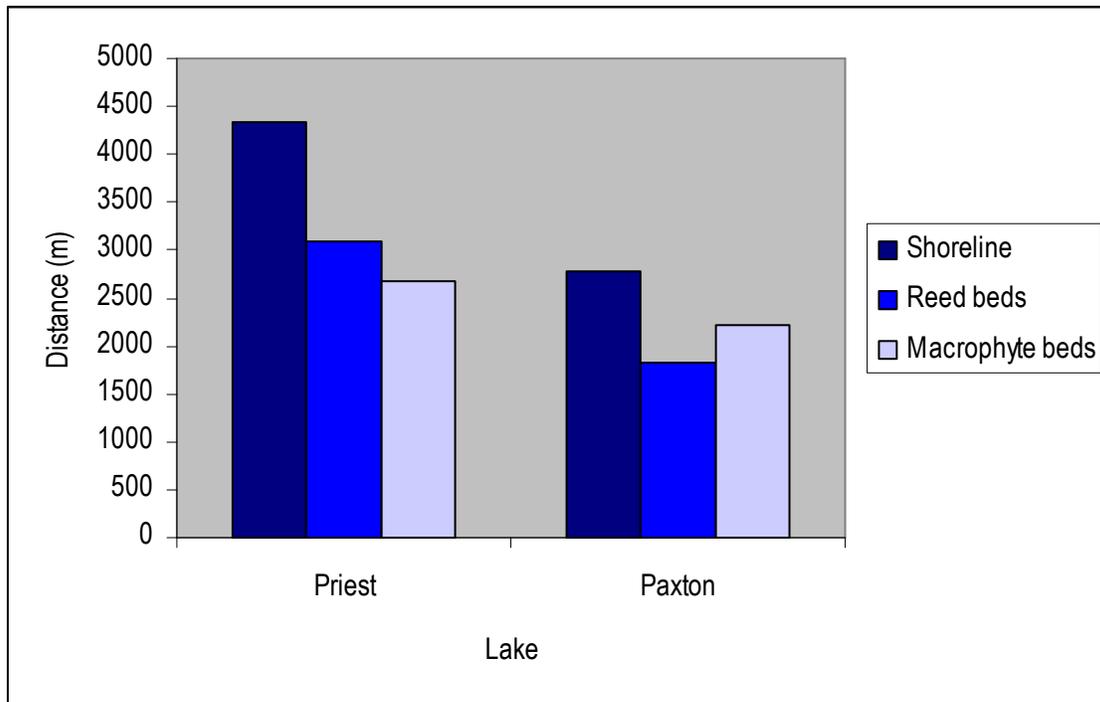


Figure 3: The length of Priest and Paxton lakes shoreline, reed and macrophyte beds.

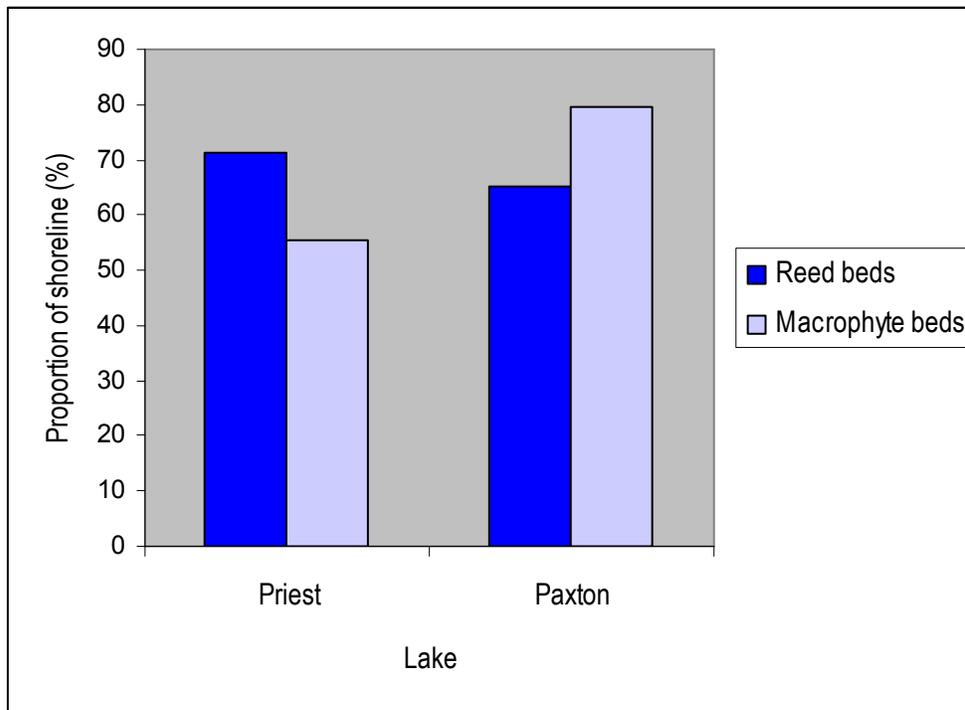


Figure 4: The proportion of Priest and Paxton lakes shoreline occupied by reed and macrophyte beds.

Table 1: Priest Lake macrophyte bed composition

Macrophyte bed number	Macrophyte species									Comments
	<i>Chara</i> sp.	<i>Najas flexilis</i>	<i>Potamogeton amplifolius</i>	<i>Potamogeton gramineus</i>	<i>Potamogeton praelongus</i>	<i>Potamogeton robbinsii</i>	<i>Potamogeton zosteriformis</i>	thin-leaved grass	<i>Utricularia vulgaris</i>	
1	√	D	D						√	
2	√		√			D			√	
3	D	√				D			√	
4	D			√		√				
5	D		√		√	D			√	
6	D	√	√			√				
7	√	√	√		√	D		√	√	
8	√		D					√		
9	D	√			√	√	√		√	
10	√		√	√		D				
11	√		√			D	√	√	√	
12	√		√			D			√	
13	√		√				√		D	low density
14		√				D			D	
15	D								D	low density
16			D						D	
17	D									
18	D		√	√					√	
19	D		√	√		√	√		D	
20					√				D	
21				√					D	low density
22			√	√					D	
23	√		√	√					D	low density
24			√	√	D	D			√	
25			√		D	√			√	
26	√		√	√	D	D				
27	√		D	D	√	D			√	
28	√		√	√					D	low density
29				D						
30	√		√						D	low density
31	√		√	D		√	√			
32	√		√	√					D	low density

√ = present
D = dominant

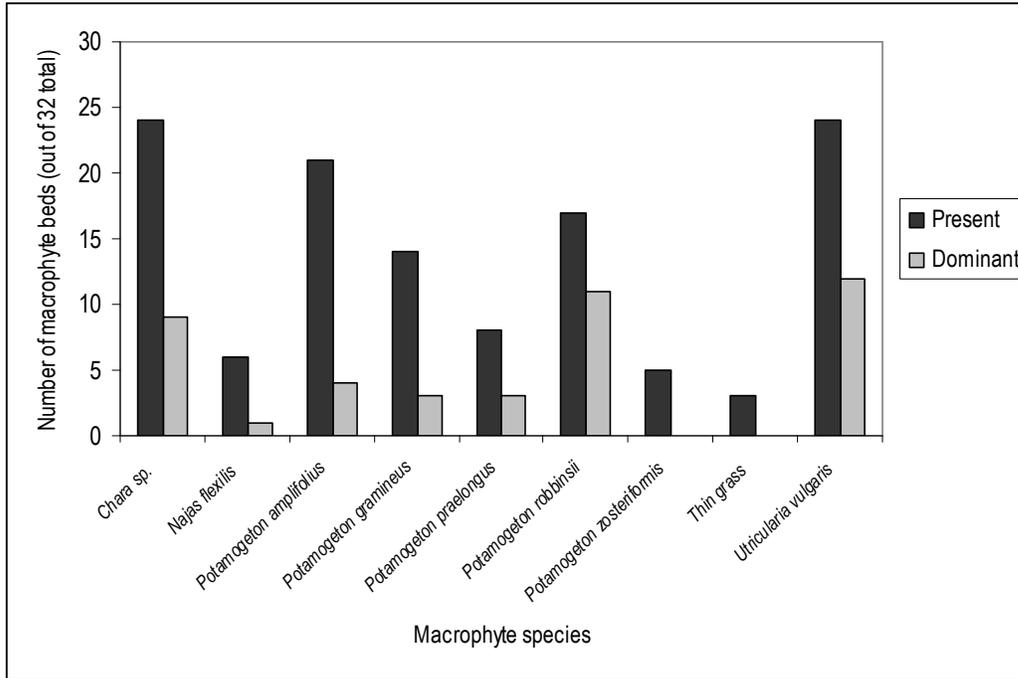
Table 2: Paxton Lake macrophyte bed composition

Macrophyte bed number	Macrophyte species									Comments
	<i>Chara</i> sp.	<i>Najas flexilis</i>	<i>Potamogeton amplifolius</i>	<i>Potamogeton gramineus</i>	<i>Potamogeton praelongus</i>	<i>Potamogeton robbinsii</i>	<i>Potamogeton zosteriformis</i>	Thin-leaved grass	<i>Utricularia vulgaris</i>	
1	√		√	√			√		D	
2	√	√	√	D						
3	√		D				√		√	
4	D		D				√		√	
5	D		√	√			√		√	
6	D		D	√	√		√		√	
7	D	√	D				√		√	
8	D	√	D				√		√	
9	D	√	D	√			√			
10	D	√	D	√			√		√	
11	D	√	D	√			D		√	
12	D	√	D	√			√		√	

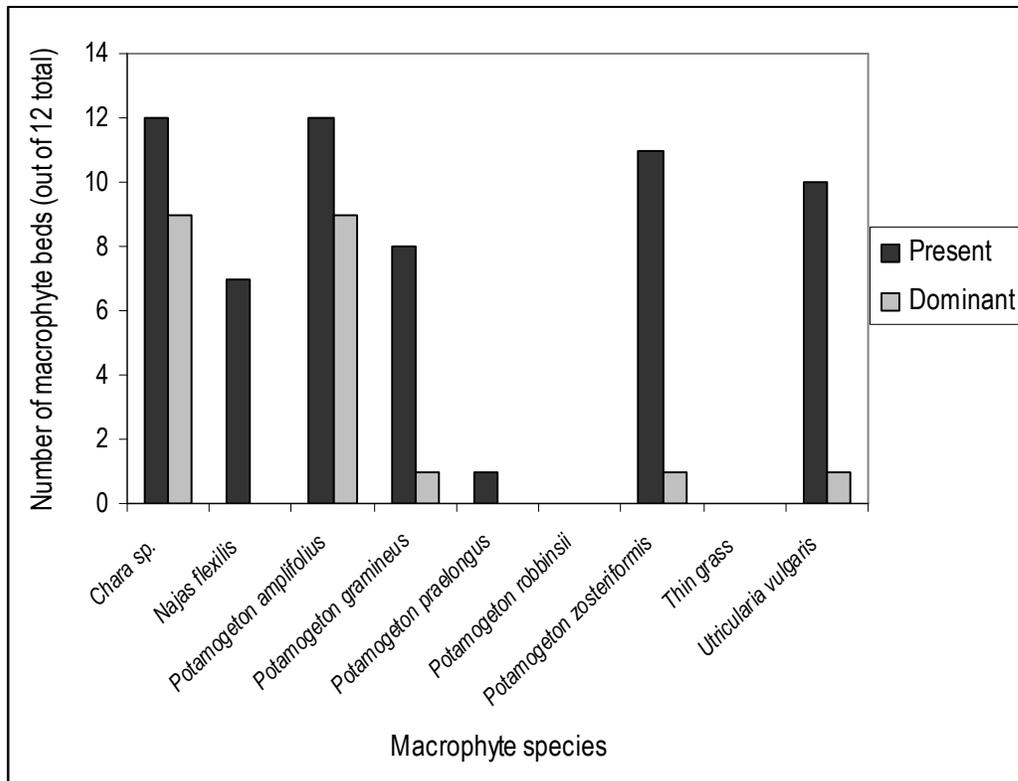
√ = present
D = dominant

Figure 5: Histogram illustrating the proportion of macrophyte beds occupied by each species.

A. Priest Lake



B. Paxton Lake



4.0 DISCUSSION

Both Priest and Paxton lakes have the majority of their littoral fringe occupied by both reed and macrophyte beds. The composition of macrophyte beds varied somewhat between lakes; however, it is perhaps the similarities between them that are more striking and most significant to the persistence of the stickleback species pairs.

A large proportion of each lake's littoral shoreline is occupied by macrophyte beds, with Paxton Lake having the most extensive ones (56% of Priest Lake and 80% of Paxton Lake). A striking similarity between their macrophyte beds is the preponderance of a species of *Chara* amongst the most common and dominant macrophyte in both lakes. *Chara* is often associated with very diverse pristine lakes which have high levels of calcium and very clear water. Beds of *Chara* tend to harbour high numbers of macroinvertebrates and there is evidence to suggest that they may ward off some predatory fish.

The abundance and composition of macrophyte beds is expected to have played a key role in the evolution of the species pairs and they are now likely critical to their continued integrity. As well as helping to maintain healthy stickleback population sizes (by providing shelter [Sillett & Foster 2000; Lehriniemi 2005], food resources [Webster & Hart 2004], and nesting sites [Kraak et al. 1999, 2000]), the habitat diversity generated by the macrophytes is essential to providing the different microhabitats which the adults prefer to use for nesting during the breeding season, when they share the littoral zone (Ridgway & McPhail 1987). This microhabitat segregation between species during the breeding season plays an important part in ensuring accurate mate choice and minimizing hybridization (Ridgway & McPhail 1984).

This work can now serve as a baseline to monitor the health of existing macrophyte beds through regular surveys of the macrophyte beds within each lake. Such observation can act as an early warning system about the health of the lakes and will serve as an important conservation tool in maintaining the integrity of the species pairs.

These surveys will also act as a baseline to conduct comparable surveys in other stickleback lakes, from which we can build our understanding of the role played by the abundance and composition of macrophytes in the evolution and persistence of benthic limnetic species pairs. This work will enable us to better understand the key factors determining their highly restricted geographic distribution. Such a survey should encompass the other extant species pair lake (Little Quarry Lake), as well as include a range of lakes containing solitary species of stickleback.

These lakes should be chosen as those sharing many other attributes with the species pair lakes e.g. physical and chemical characteristics and fish community. A comparative survey of fish fauna in species pair or solitary species lakes found a striking difference: while species pair lakes were only inhabited by cutthroat trout and stickleback, single species lakes almost always harboured a more diverse fish fauna, despite no significant differences between the lakes in abiotic factors (Vamosi 2003). A similar study investigating the impact of variable macrophyte communities in lakes would surely uncover further insights into pertinent conditions for the evolution and persistence of the species pairs.

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6.0 APPENDICES

Appendix A: Specimen of *Chara* sp.



Appendix B: Specimen of *Najas flexilis*



Appendix C: Specimen of *Potamogeton amplifolius*



Appendix D: Specimen of *Potamogeton gramineus*



Appendix E: Specimen of *Potamogeton praelongus*



Appendix F: Specimen of *Potamogeton robbinsii*



Appendix G: Specimen of *Potamogeton zosteriformis*

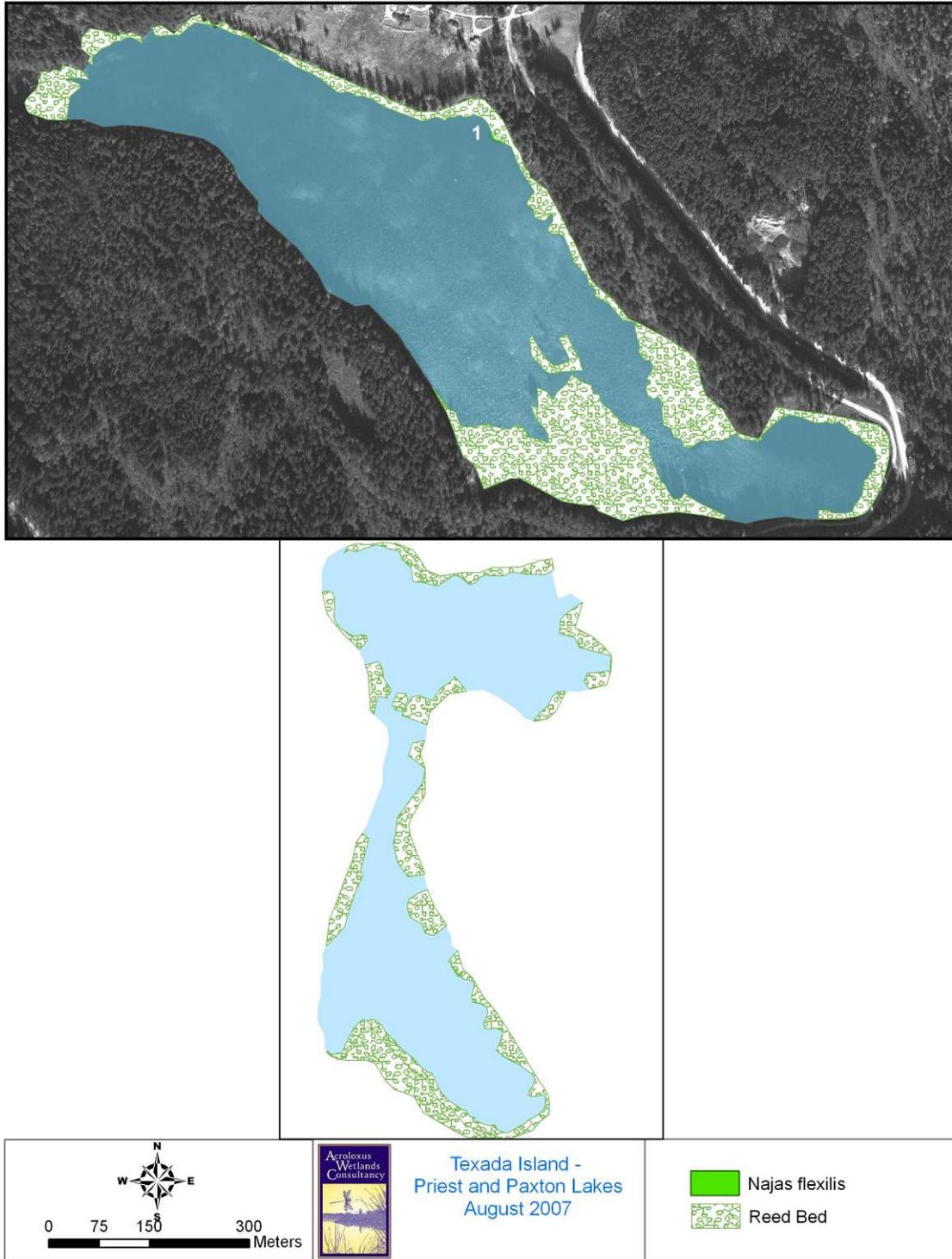


Appendix H: Specimen of thin-leaved grass

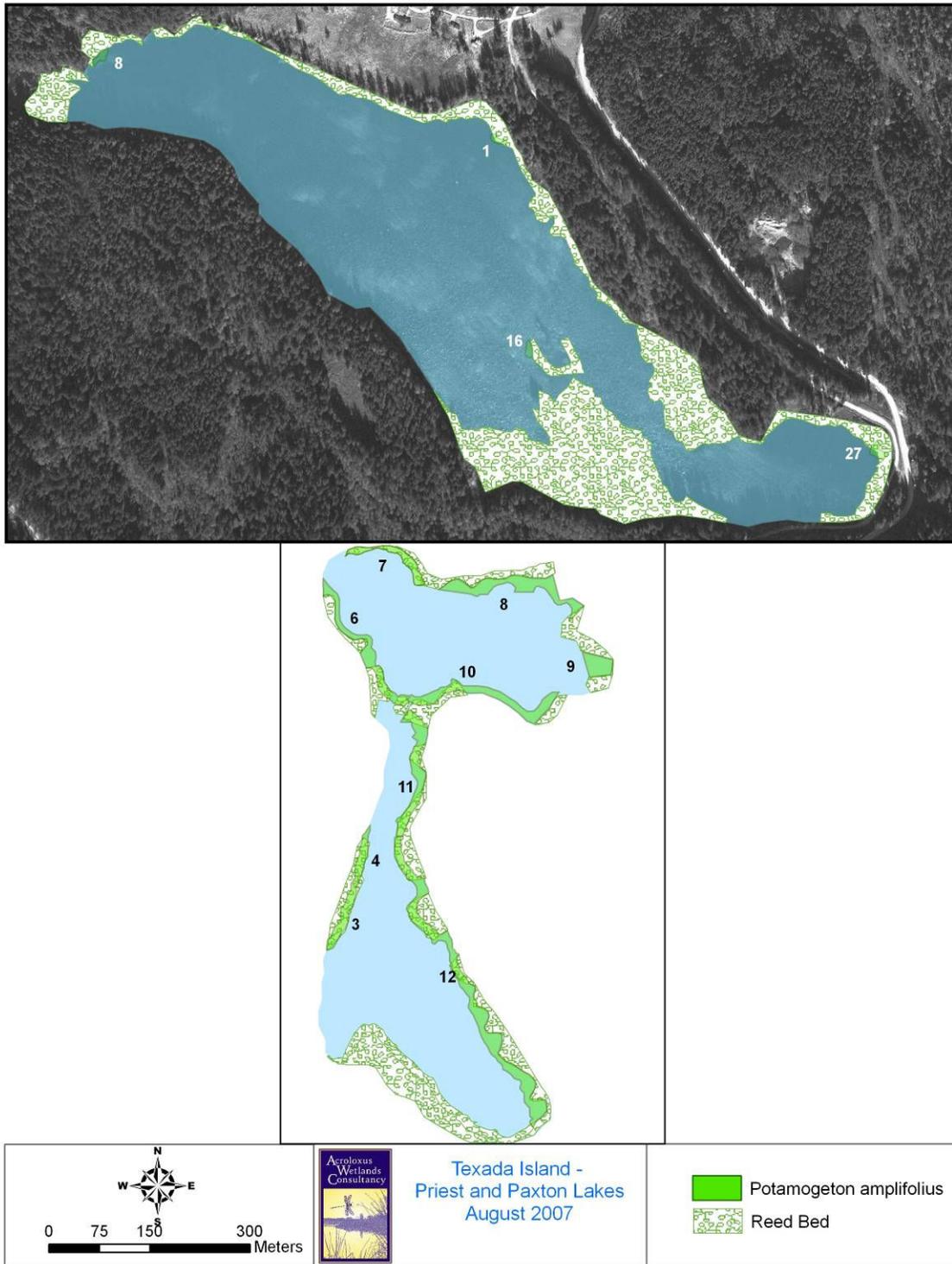


Appendix I: Specimen of *Utricularia vulgaris*

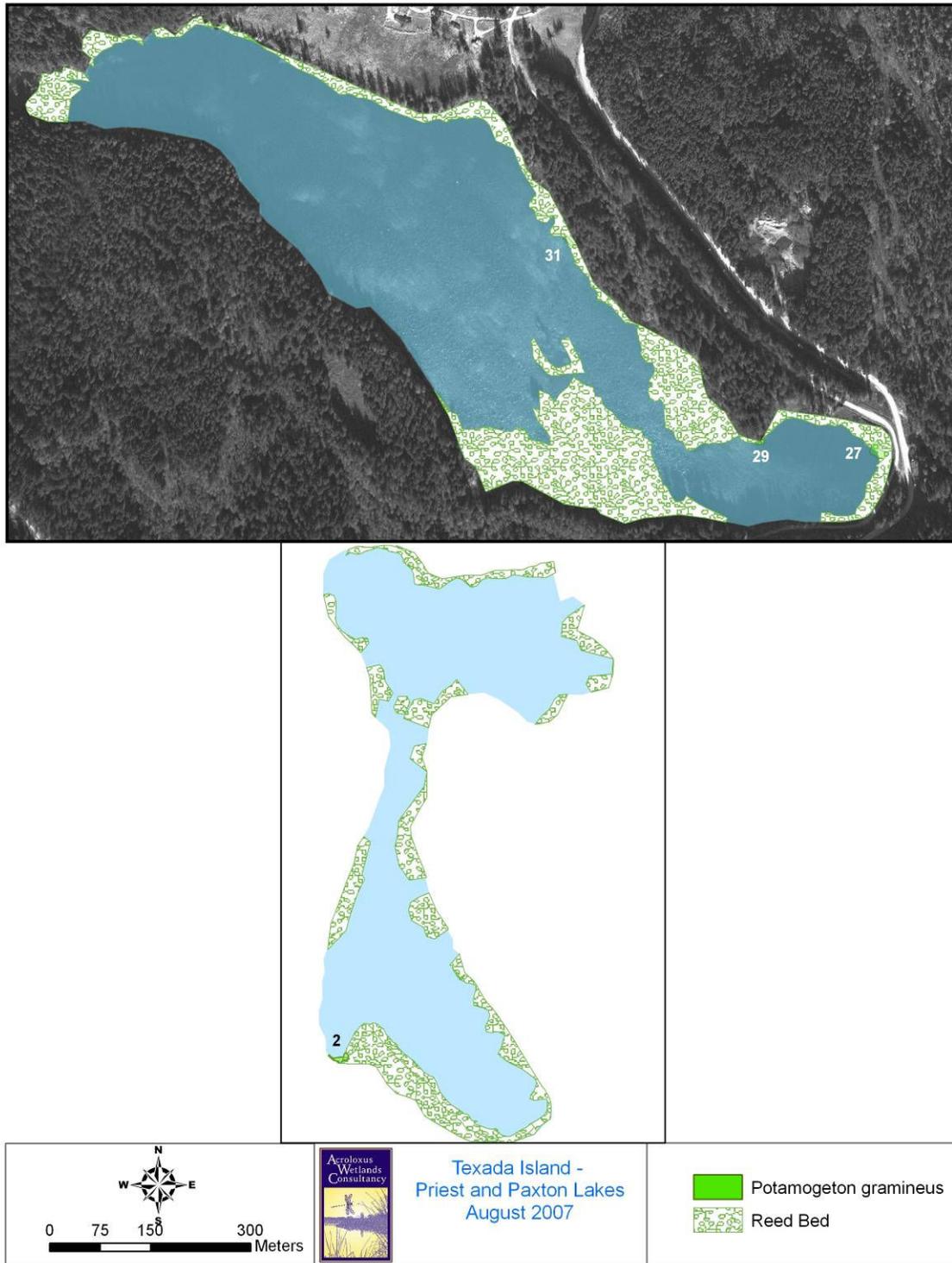




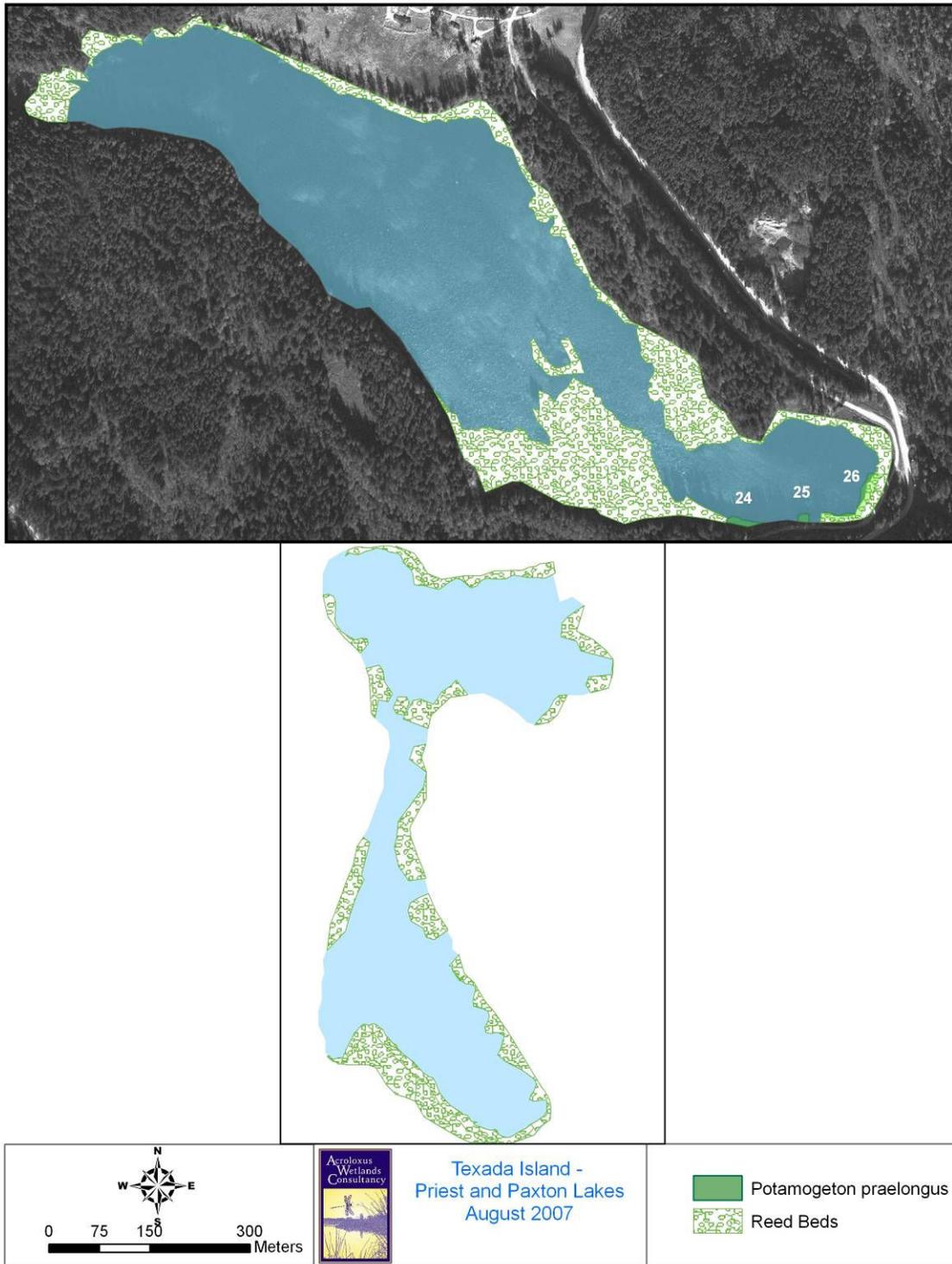
Appendix K: Map of macrophyte beds where *Najas flexilis* is dominant in Priest and Paxton lakes, Texada Island, BC.



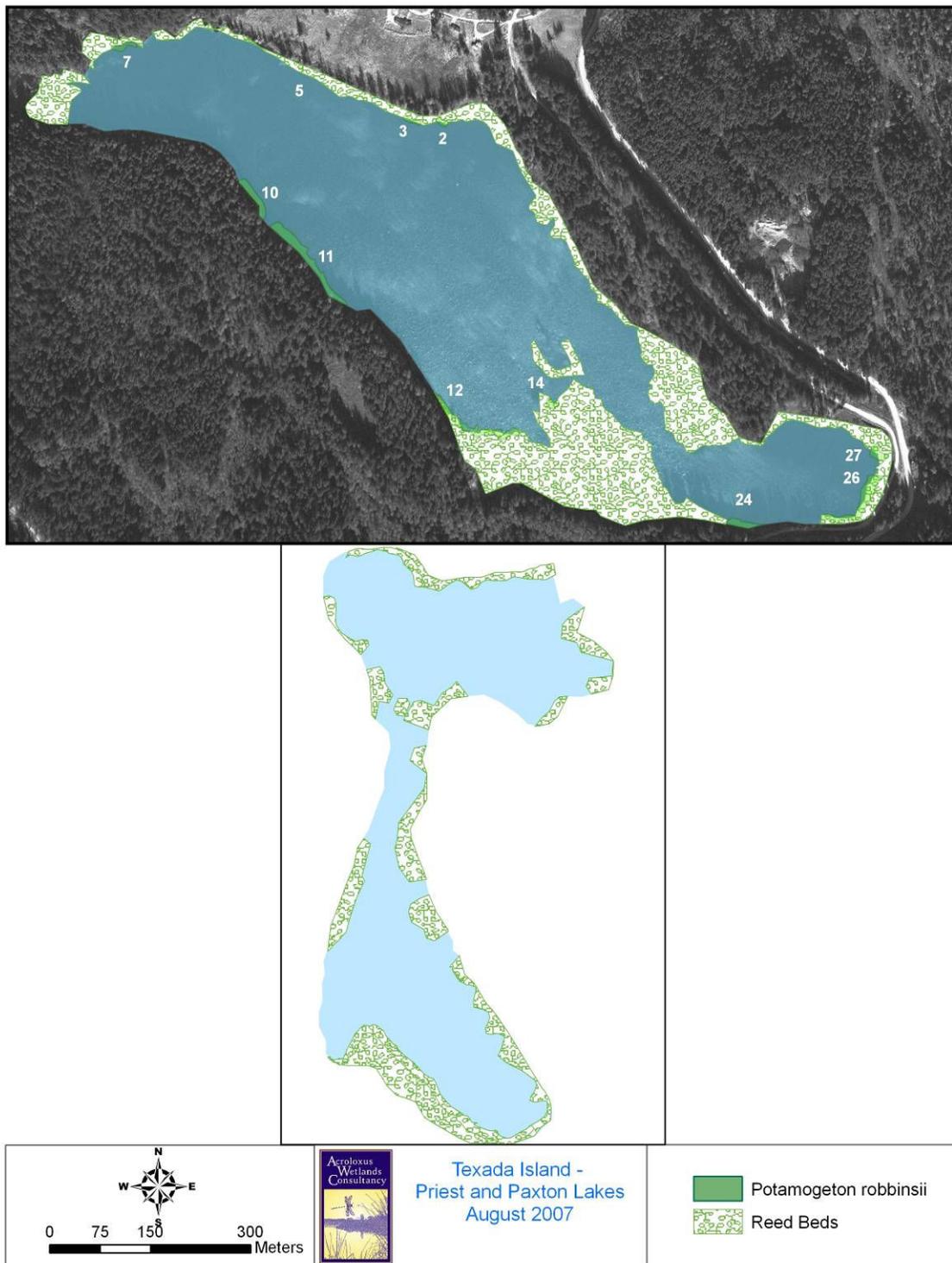
Appendix L: Map of macrophyte beds where *Potamogeton amplifolius* is dominant in Priest and Paxton lakes, Texada Island, BC.



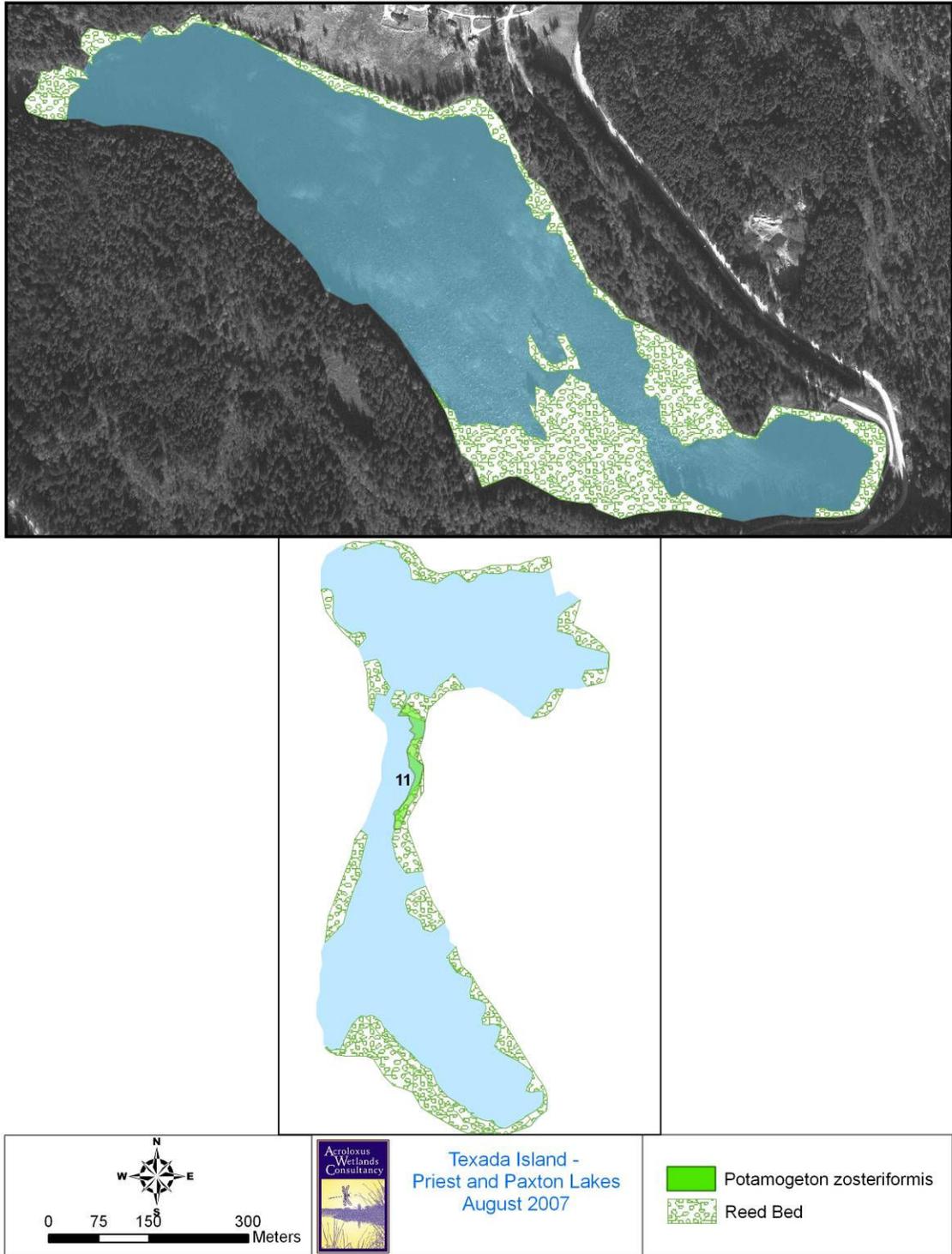
Appendix M: Map of macrophyte beds where *Potamogeton gramineus* is dominant in Priest and Paxton lakes, Texada Island, BC.



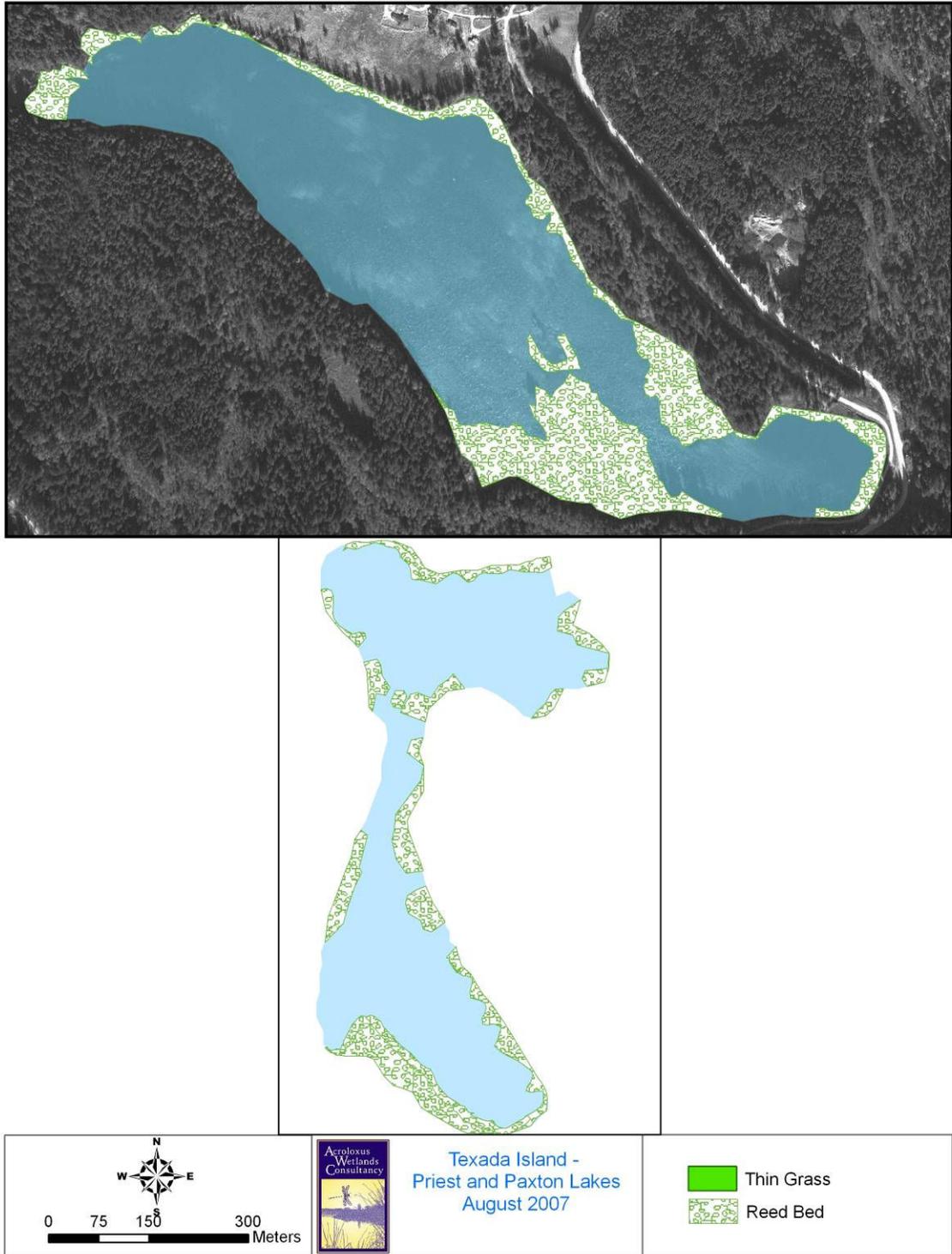
Appendix N: Map of macrophyte beds where *Potamogeton praelongus* is dominant in Priest and Paxton lakes, Texada Island, BC.



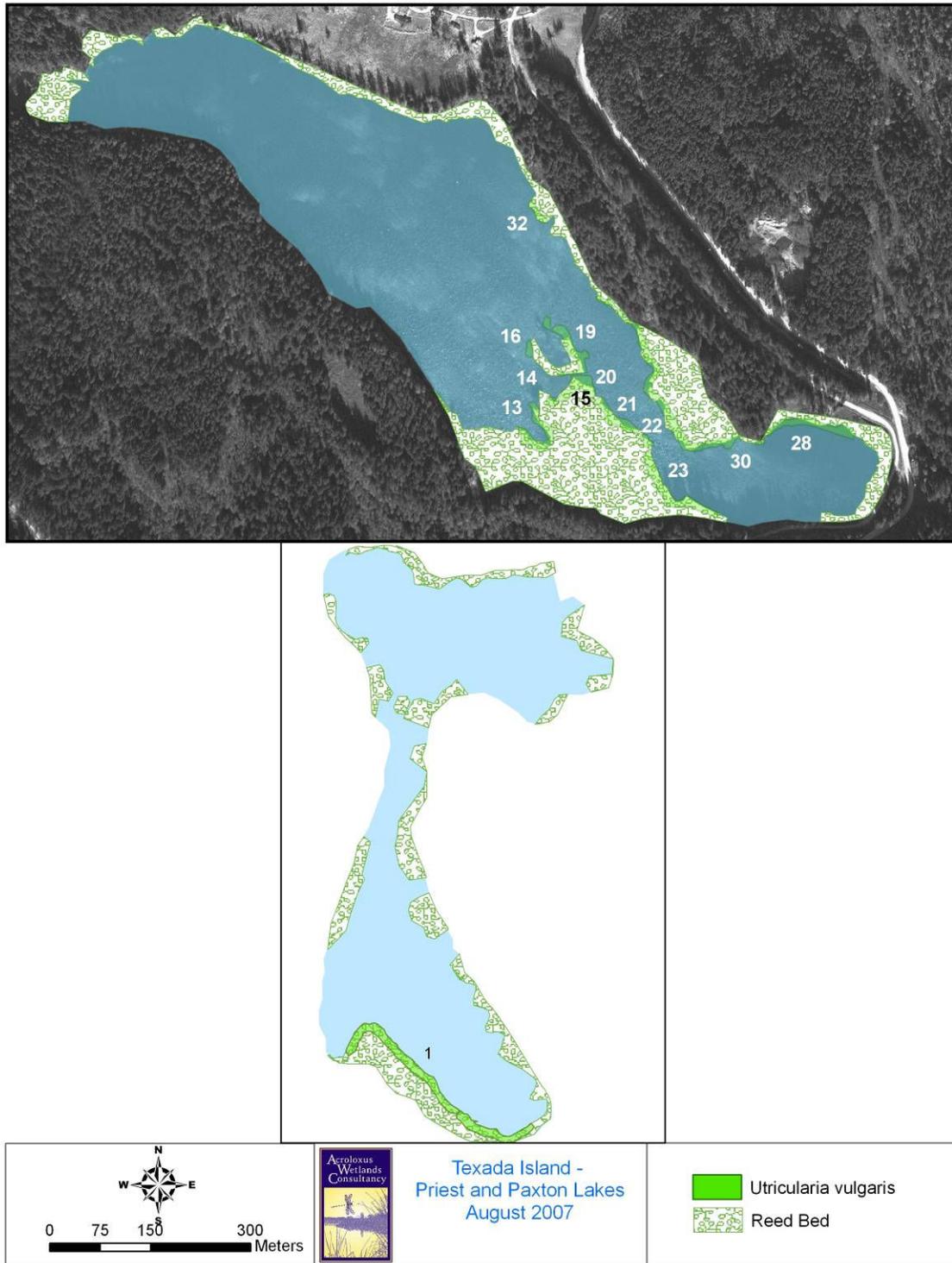
Appendix O: Map of macrophyte beds where *Potamogeton robbinsii* is dominant in Priest and Paxton lakes, Texada Island, BC.



Appendix P: Map of macrophyte beds where *Potamogeton zosteriformis* is dominant in Priest and Paxton lakes, Texada Island, BC.



Appendix Q: Map of macrophyte beds where thin-leaved grass is dominant in Priest and Paxton lakes, Texada Island, BC.



Appendix R: Map of macrophyte beds where *Utricularia vulgaris* is dominant in Priest and Paxton lakes, Texada Island, BC.